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Report

Automictic Reproduction in Interspecific Hybrids of Poeciliid Fish

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Summary

Automixis, the process whereby the fusion of meiotic products restores the diploid state of the egg, is a common mode of reproduction in plants but has also been described in invertebrate animals [1, 2]. In vertebrates, however, automixis has so far only been discussed as one of several explanations for isolated cases of facultative parthenogenesis [3, 4]. Analyzing oocyte formation in F1 hybrids derived from *Poecilia mexicana limantouri* and *P. latipinna* crosses (the cross that led to the formation of the gynogenetic *Poecilia formosa* [5, 6]), we found molecular evidence for automictic oocyte production [7]. The mechanism involves the random fusion of meiotic products after the second meiotic division. The fertilization of diploid oocytes gives rise to fully viable triploid offspring. Although the automictic production of diploid oocytes as seen in these F1 hybrids clearly represents a preadaptation to parthenogenetic reproduction [8], it is also a powerful intrinsic postzygotic isolation mechanism because the resulting next generation triploids were always sterile. The mechanism described here can explain facultative parthenogenesis [9], as well as varying ploidy levels reported in different animal groups [10]. Most importantly, at least some of the reported cases of triploidy in humans [11] can now be traced back to automixis.

Results

A basic principle of reproduction is a reorganization of chromosomes without alternations of ploidy. Several mechanisms have been described that restore diploidy, the most common ploidy level in animals. In amphimixis, meiosis and syngamy alternate [1]. In apomixes, meiosis is repressed and the oocyte is produced by mitosis, whereas in automixis, meiosis is maintained and the diploid stage is restored after meiosis either by the fusion or duplication of meiotic products. In premeiotic endomitosis, the genome is doubled before meiosis and then segregated [1, 2]. Apomixis and premeiotic endomitosis do not lead to genetic variation of the resultant eggs [7]. Automixis, however, can lead to variable offspring because segregation and recombination take place between nonidentical homologous chromosomes.

In vertebrates, bisexual reproduction (amphimixis) clearly dominates reproductive modes. There are, however, several species within the lower vertebrates that reproduce unisexually [12]. The production of unreduced oocytes is a prerequisite to parthenogenetic reproduction and, therefore, of paramount interest to researchers of the evolution of sex.

The Amazon molly (*Poecilia formosa*), a gynogenetic fish, was the first vertebrate discovered to reproduce clonally [13]. Like all other unisexual organisms, it originated from a hybridization event [14, 15], in this case of a *Poecilia mexicana limantouri* female and a *P. latipinna* male [5, 6]. We analyzed five of these interspecific crosses that included a total number of 41 F1 females plus their 570 offspring (see Table S1 in the Supplemental Data available online). Thirty-eight females were *P. m. limantouri* × *P. latipinna* F1 hybrids (mex/lat) and three came from the reciprocal cross, *P. latipinna* × *P.m. limantoui* (lat/mex). The first generation F1 hybrids were phenotypically (body shape, dorsal-fin-ray counts, and coloration) intermediate between *P. m. limantouri* and *P. latipinna,* and the females closely resembled *P. formosa*. Nineteen of the 38 mex/lat females analyzed (50%) had all-triploid offspring, whereas only a single female (2.6%) showed exclusively diploid offspring. All other mex/lat families analyzed included diploid as well as triploid offspring, but triploid offspring prevailed (74%). In the lat/mex hybrids, diploid offspring were more common (94%) than were triploid: Only one female had triploid offspring. Individual mex/lat crosses also differed in the proportions of the sexes produced and in ploidy-level frequencies (Table S1).

We then used Black molly males to visually screen for paternal genetic contributions in the next generation. The offspring derived from the crosses of the female F1 hybrids showed very different pigmentation patterns, ranging from nonspotted to black. As expected, the pigmentation pattern was linked to the ploidy level of the offspring, with triploid males and females being significantly lesser pigmented than were diploids. Diploid unspotted females, an indication of gynogenetic reproduction (the exclusion of the paternal genome), were never observed. Microchromosomes could not be detected in the animals' karyotypes.

Although all F1 hybrids had well-developed ovaries and were fertile, their offspring differed in fertility: 28 out of 48 diploid females (58.1%) had very well-developed ovaries and produced offspring when mated to Black molly or *P. mexicana* males, but 269 out of 307

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triploid females (88%) showed no gonadal development. Triploids mated with Black molly or *P. mexicana* males never produced any offspring. The same pattern was true for males, with diploids being fertile when mated to female *P. mexicana* and triploids being sterile.

Sixteen families that included 151 triploid offspring were analyzed with multilocus DNA fingerprints (Figure 1, Table 1). Notably, the triploid offspring of F1 hybrid females did not exhibit all maternal bands (Figure 1), even though they did not show any aberrations from the expected set of 69 chromosomes. Triploid offspring inherited on average 85% of the maternal bands (Table 1). The combined probability of a band to be lost was close to 15% (Table 1). Statistical analysis found automixis (a random fusion of products from the same meiosis) to be the most likely mechanism for the restoration of diploidy in F1 hybrid eggs (Figure 2).

In microsatellite analyses of 109 triploid offspring from heterozygous mothers, 24 cases of the loss of heterozygosity (LOH) were detected at seven loci (22%, Table 2). Separate statistical analyses for each locus revealed that neither unreduced oocyte formation (expected LOH = 0%) nor gamete duplication (expected LOH = 100%) could explain the LOH rate found in the microsatellite data (Figure 2).

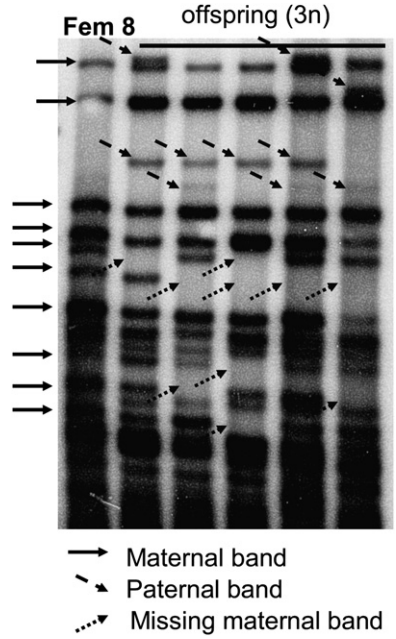

Figure 1. Multilocus DNA Fingerprint of a Female F1 Hybrid and Her Triploid Offspring

Black continuous arrows depict maternal bands, dashed arrows depict additional bands in the offspring (paternal bands), and dotted arrows depict missing maternal bands.

Discussion

In an experimental approach to understand the origin of asexual species, we repeated the cross of *P. mexicana*

Table 1. Result of the Multilocus DNA Fingerprint Analyses

Family	ID	Cross	Description	Percentage of Bands Shared with Maternal Genome		Band's Probability to Be Lost		Nba	Ni
				Mean	SD	Mean	SD		
1	1846	1	*P. mex*$_{VI/5}$/*P. lat*$_{IX/24}$	79.2	12.6	20.8	20.2	12	6
2	2190-2	2	*P. mex*$_{VI/5}$/*P. lat*$_{IX/24}$	92.2	11.8	7.8	10.9	17	9
3	2190-4	2	*P. mex*$_{VI/5}$/*P. lat*$_{IX/24}$	94	6.1	5.6	8.3	9	6
4	2190-8	2	*P. mex*$_{VI/5}$/*P. lat*$_{IX/24}$	91.4	5.7	8.6	12.7	16	8
5	2255-3	2	*P. mex*$_{VI/5}$/*P. lat*$_{IX/24}$	71.8	9.4	28.2	24.3	13	9
6	2255-8	2	*P. mex*$_{VI/5}$/*P. lat*$_{IX/24}$	85	10.9	16.7	23.9	12	5
7	2281-1	2	*P. mex*$_{VI/5}$/*P. lat*$_{IX/24}$	88.2	8.3	12.4	15.7	10	9
8	2281-4	2	*P. mex*$_{VI/5}$/*P. lat*$_{IX/24}$	90.9	11.5	9.1	14.1	6	11
9	2282-1	2	*P. mex*$_{VI/5}$/*P. lat*$_{IX/24}$	84.3	9.1	15.3	12.2	18	12
10	2282-3	2	*P. mex*$_{VI/5}$/*P. lat*$_{IX/24}$	85.3	8.6	15.2	13.1	12	17
11	2282-4	2	*P. mex*$_{VI/5}$/*P. lat*$_{IX/24}$	84.7	10.6	15.3	12.3	16	11
12	2466	3	*P. mex*$_{VI/5}$/*P. lat*$_{IV/5}$	86.4	11	13.6	6.7	12	18
12	2466b	3	*P. mex*$_{VI/5}$/*P. lat*$_{IV/5}$	83.3	8.3	16.7	13.4	15	5
13	2468	3	*P. mex*$_{VI/5}$/*P. lat*$_{IV/5}$	89.6	7.5	11.7	13.4	12	5
14	2511	3	*P. mex*$_{VI/5}$/*P. lat*$_{IV/5}$	79.6	18	20.5	23.2	11	8
15	2512	3	*P. mex*$_{VI/5}$/*P. lat*$_{IV/5}$	80.8	6.6	19.1	18.2	16	8
			Total mean	85.42	9.75	14.79	15.16	12.94	9.19
			Total SD	5.76	3.03	5.75	5.36	3.21	3.92
			Expected for unreduced oocytes	100		0			
			Expected for duplication after first division	50		50			
			Expected for random fusion after meiosis	83		17			
A	2504		*P.lat*$_{VI/5}$/*P. mex*$_{IV/}$	88.3	8.4	11.7	21	15	4

Given are the percentage of bands shared between mother and offspring (mean and standard deviation [SD]) and each band's probability to be lost during meiosis (mean and SD). Also given are the number of bands analyzed (Nba) and the number of offspring analyzed (Ni). Family 12 (2466/2466b) appears twice because the offspring from this female had to be analyzed on two different gels. Total means and SD are given for the *Poecilia mexicana*/*Poecilia latipinna* crosses.

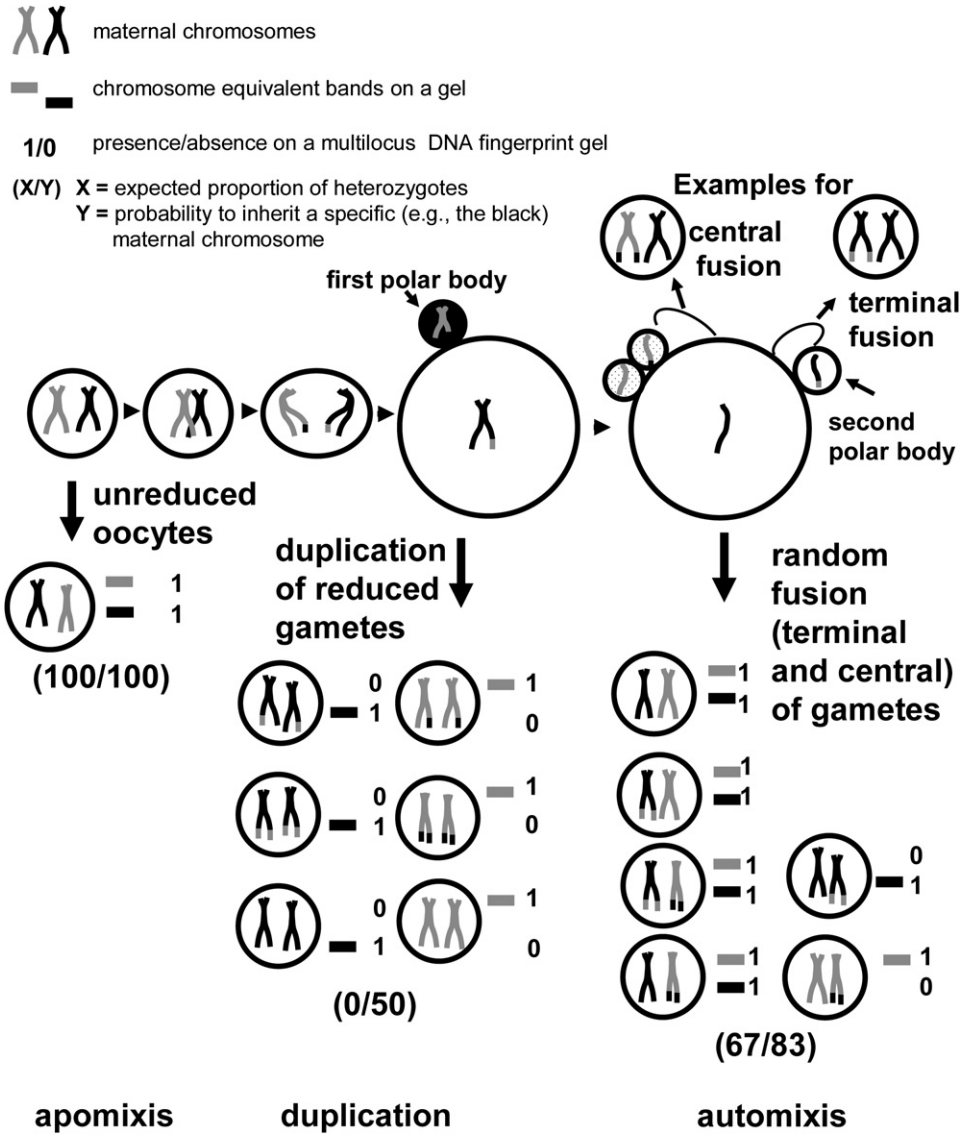

Figure 2. Schematic Drawing of Diploid-Oocyte Formation in Vertebrates

The three different possibilities for recovering diploidy discussed in the paper are shown: unreduced oocytes, duplication after the first meiotic division, and the random fusion of oocytes (a mixture of central and terminal fusion) after the second meiotic division. In addition, the resulting diploid oocytes for all scenarios as well as the expected proportions of heterozygotes and the probability of the offspring to inherit a specific maternal chromosome are given.

limantouri and *P. latipinna* that has most likely led to the gynogenetic *Poecilia formosa*. The F1 hybrids produced diploid as well as triploid offspring, and thus they were able to produce haploid as well as diploid eggs. Diploid offspring shared about 50% of all bands (according to multilocus DNA fingerprints, as well as microsatellites [data not shown]) with their mother. Triploids, however, did not inherit all maternal bands.

The inheritance of all maternal genetic material would be expected for diploid eggs produced by premeiotic endomitosis or apomixis [7], which were, hitherto, the only known mechanisms leading to the production of diploid eggs in obligate parthenogenetic vertebrates [7, 16, 17]. The patterns of band loss in multilocus DNA fingerprints and LOH in microsatellites in the triploid offspring of F1 diploid females found in this study can best be explained by the occurrence of some form of segregation in the process of oocyte formation [7]. From theoretical considerations, three different possibilities for the restoration of diploidy in the oocytes would lead to triploid offspring (Figure 2): (1) The formation of unreduced eggs (apomixis) or the fusion of oocytes after the first meiotic division would lead to diploid oocytes with all genetic material being inherited from the mother (100%) and to no loss of heterozygosity (0%); (2) a duplication after the first meiotic division would lead to offspring that only inherit 50% of the bands from the mother and to 100% LOH of maternal genes; and (3) automixis can be subdivided into terminal and central fusion of meiotic products (Figure 2). In terminal fusion, the oocyte fuses with the second polar body, whereas in central fusion, the oocyte fuses with a first polar body. A random fusion of reduced gametes, after meiosis was completed (a mixture of terminal as well as central

Table 2. Summary of Microsatellite Analysis Results of Heterozygous Females and Their Triploid Offspring

				Gamete Duplication	Terminal Fusion	Random Fusion	Apomixis (No Meiosis)
Locus	Nt	No	R	r = 1	r = 2/3	r = 1/3	r = 0
mAGT31	29	5	0.17	<0.0001	0.0004	0.23	0.0518
mATG32	7	2	0.29	= 0.021	0.2861	1	0.4615
mATG38	14	3	0.21	<0.0001	0.025	0.68	0.222
mATG78	15	5	0.33	= 0.0002	0.143	1	0.421
mATG89	13	2	0.15	<0.0001	0.0093	0.3955	0.48
mCA20	10	1	0.10	<0.0001	0.0198	0.3034	1
mCA32	47	9	0.19	<0.0001	<0.0001	0.1622	0.0026
Total	109	24	0.22	<0.0001	<0.0001	0.0008	<0.0001

Given are the microsatellite locus used for the analyses (Locus), the number of offspring from heterozygous mothers (Nt), the number of transitions to homozygosity (No), the observed rate of transitions to homozygosity (R), the expected rate of transitions to homozygosity under the different scenarios (gamete duplication, terminal fusion, random fusion, apomixis) (r), and the p values for the comparison of R to r (Fisher's test). The highest p value for each locus is marked in underlined typeface.

fusion) (Figure 2), would result in 83% inheritance of maternal bands and to 0%–33% LOH [18]. Our results (85% inheritance of maternal bands, 22% LOH) were significantly different from the expected number of shared bands and LOH in unreduced eggs and from duplication after the first meiotic division. In fact, the values were consistent with the expectation for a random fusion of oocytes after the second meiotic division. Automixis with a random fusion of meiotic products, therefore, is the most likely explanation for the formation of diploid eggs in F1 hybrids.

Other potential explanations for the loss of heterozygosity include the ameiotic recombination or double fertilization of the oocyte. Rates of ameiotic recombination, however, are generally very low and lead to only very few LOHs per generation (0.00016 per locus per generation in Daphnia [19]). This could by far not explain the 22% rate of LOH that was observed in the triploid offspring of the F1 hybrids. Moreover, in *P. formosa*, LOH was never observed in several hundred individuals that were analyzed with the same microsatellites, including field-captured and laboratory-bred fish [20–22]. Ameiotic recombination, therefore, appears to be an unlikely explanation for our results.

Dispermy, the fertilization of a haploid oocyte by two sperm cells, or diandry, the fertilization of a haploid oocyte with a diploid sperm, are two mechanisms that have been postulated to result in triploidy [23]. Both can be excluded in our study because offspring derived from this type of reproduction should share only around 33% of their bands with their mothers. In this study, however, the proportion of shared bands in the multilocus DNA fingerprints (85%) and the rate of heterozygosity for maternal genes in the microsatellite analyses (78%) was much higher. Our results clearly point to a maternal origin of the additional set of chromosomes in the triploid offspring.

In contrast to studies of facultative parthenogenesis, which have also concluded that automixis might be involved in the diploid-oocyte formation [3, 4], we present experimental evidence for automixis in vertebrates that is likely to occur in natural populations. For the first time, sample sizes allow for precise statistical analyses of the mechanism involved in the restoration of ploidy levels (the random fusion of meiotic products).

The crosses analyzed in this study mimicked the initial hybridization event leading to the formation of the gynogenetic Amazon molly, *Poecilia formosa*. In vertebrates, unisexual reproduction is clearly correlated to hybridization. All unisexually reproducing vertebrates are hybrids [12, 14]. This might be due to the fact that the combination of foreign genomes (hybridization) can compromise meiosis, leading to unreduced oocytes [24]. Polyploidy might, therefore, rescue fertility in hybrids [25]. In fish, e.g., hybridization as well as polyploidy and unisexual reproduction are relatively common [12, 26, 27]. Two different modes of unisexual reproduction predominate in fish: gynogenesis, in which the egg is produced apomictically [8, 28], and hybridogenesis, in which the egg is produced hemiclonally and only the maternal genome is transferred unaltered to the egg [29] (for an overview, see [14]). In some species, diploids produce hybridogenetically [30, 15], whereas triploids reproduce gynogenetically [31, 32]. The production of diploid eggs is clearly a preadaptation to gynogenetic reproduction. Diploid eggs, however, are also a mechanism for preventing hybridization. Hybrids producing triploid offspring (because of the fertilization of diploid ova) clearly suffer a fertility loss because triploids are generally sterile. Triploid sterility should result in a high selective pressure against hybridization. In the case analyzed here, 50% of all hybrids had only triploid offspring and therefore no long-term reproductive output. In addition, the majority off all offspring derived from hybrid females that produced diploid as well as triploid offspring were triploids and hence sterile. Only a single female produced exclusively diploid offspring. We suggest that hybrids suffer from lower fertility than their pure parental species because they produce a high percentage of sterile triploid offspring because of altered meiosis. This would be a much simpler mechanism for intrinsic postzygotic isolation than the inferred single genes that reinforce reproductive isolation and that receive significant attention in the literature [33]. Large-scale investigation of hybrid-offspring ploidy levels would help clarify its distribution and evolutionary potential.

Even though there are no known cases of self-sustaining vertebrate automicts in nature, infrequent automixis is very likely overlooked in routine population genetic surveys. Automixis might, therefore, be more common than has been recognized to date. It can explain facultative parthenogenesis in sharks [3], monitor lizzards [9, 34], and other species of reptile [35] but might be equally important in the evolution of obligate parthenogens. The

parental species of *P. formosa*, for example, co-occur and could therefore hybridize in their natural habitat of Northeast Mexico. These populations, however, have never been screened for hybrids and triploids. Automixis might have led to a successful initial *P. formosa* genotype. Automixis also explains the inheritance of pigmentation and sex determination in parthenogenetic turkey strains [4] and polyploidisation events observed in salamanders [10]. In humans, triploidy is a common chromosome aberration (2%) and is responsible for a large number of spontaneous first-trimester abortions [36]. The mechanism leading to triploidy in humans is unclear, and automixis has only recently been considered [37, 38]. It could, for instance, explain the LOH observed in a study of recurrent maternal triploidy [36] and motivate further analyses in the future.

Conclusions

We present conclusive experimental data for automixis in vertebrates. F1 hybrids of *Poecilia mexicana* and *P. latipinna* regularly produced unreduced, diploid oocytes that after fertilization led to viable but sterile triploid offspring. Our key findings suggest that automixis might be a mechanism that, on the one hand, is a preadaptation to facultative as well as obligate parthenogenetic reproduction but might also lead to an intrinsic postzygotic isolation mechanism in hybrids. Automictic diploid-oocyte formation can also explain a number of reports of polyploidy in vertebrates, including humans, in which triploidy is the most common reason for abortion during the first trimester. In summary, we propose a mechanism that can easily explain the formation of unisexual species, as well as the lower fitness often observed in hybrids.

Supplemental Data

Experimental Procedures and one table are available at http://www.current-biology.com/cgi/content/full/17/22/1948/DC1/.

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